The larval morphology of European *Chironomus* species *C. acidophilus* Keyl and *C. crassimanus* Strenzke (Diptera: Chironomidae)¹

by

C. J. WEBB * and A. SCHOLL **

With 8 figures

Abstract

A description is given of the larval morphology of two European species of *Chironomus, C. acidophilus* and *C. crassimanus,* the former of which is recorded from Switzerland for the first time. Body and head capsule characters are described, with special attention being paid to larval ventromental plates. Characters of use in discriminating the larvae of *C. acidophilus* and *C. crassimanus* from those of other European species are identified and their overall morphological similarity to larvae of other members of the *pseudothummi* cytological complex is assessed by means of a cluster analysis.

INTRODUCTION

More than 50 valid European species of *Chironomus* have been described (FITTKAU & REISS 1978, LINDEBERG & WIEDERHOLM 1979). Although larvae of these species represent one of the most widespread and successful groups of freshwater macroinvertebrates, immatures are difficult to identify on the basis of their morphology and detailed morphological information is available for less than half of the recognized taxa (LINDEBERG & WIEDERHOLM 1979; BRENNAN 1981, WEBB & SCHOLL 1985).

¹ Dedicated to Prof. Dr. W. Wülker on the occasion of his 65th anniversary.

^{*} Northern Territory University, GPO Box 1341, Darwin, NT 5794, Australia.

^{**} Universität Bern, Baltzerstrasse 3, Bern, CH-3012, Switzerland.

The most extensive effort, to date, at morphological identification of European *Chironomus* larvae was made by WEBB & SCHOLL (1985). These authors presented data on a wide range of morphological characters for twenty-six cytologically identified species, and wrote a key which discriminated the taxa investigated. This key included all of the 21 species of *Chironomus* s. str. which had been recorded from Switzerland at that time (RYSER *et al.* 1980, 1983; WÜLKER *et al.* 1981, 1983). After the publication of this key, one of the present authors (AS) found another species from Switzerland, cytologically identified as *C. acidophilus* Keyl, 1960, which previously had been reported only from its type locality of Reinbek, near Hamburg, Western Germany. Reinbek is also the only known locality of another species, *C. crassimanus* Strenzke, 1959 which is related to *C. acidophilus*.

C. acidophilus was primarily described on the basis of larval karyology, although KEYL did mention that the species had "*thummi*-type" larvae, one of a limited number of "larval types" first recognized by LENZ (1954) and characterized by the possession of two pairs of long, roughly equal-sized tubules arising from the ventral surface of the eleventh body (eight abdominal) segment and the absence of lateral tubules on body segment ten. In contrast to *C. acidophilus, C. crassimanus* was first described on imaginal characters alone. Subsequently KEYL & KEYL (1959) gave details of larval karyology of *C. crassimanus* and in 1962 KEYL placed this species and *C. acidophilus* in the *pseudothummi*-complex, one of the three main cytological complexes to which European Chironomus species are currently referred (MARTIN 1979; WÜLKER 1980).

It is clear that very little is known about the larval morphology of *C. acidophilus* and *C. crassimanus*. The aim of this paper is, therefore, to provide detailed information on the morphological characteristics of these two species which could be used in their identification. Special attention has been paid to the morphology of ventromental plates, as these structures, which play an important role in the processes of silk-spinning (WEBB *et al.* 1981), have been a useful source of diagnostic features in larvae of *Chironomus* and other genera (e.g. WEBB 1980, WEBB & SCHOLL 1985, 1987, WEBB & MARTIN 1987, WEBB *et al.* 1985, 1987).

MATERIAL AND METHODS

Studies were carried out on fourth instar larvae. The following material was used.

C. acidophilus: eight larvae collected in April 1984 in the Chlepfibeeri Moos near Aeschi/SO, Switzerland; six larvae from the Thienemann collection, labelled "*Chironomus meigeni*, Zucht aus Tonteich bei Reinbek, 19.V.1950, Coll. A. Thienemann, leg. K. Strenzke", having on a second label the note handwritten by K. Strenzke "Zucht bis 18.VII.1950".

C. crassimanus: ten larvae from the Strenzke collection, labelled "*Ch. crassimanus,* Coll. Strenzke 13.X.1958, Reinbeck, Tonteich, pH 3,05" and ten larvae of the Strenzke collection, labelled "*Chironomus crassimanus,* 898. Coll. et leg. K. Strenzke, Reinbeker Tonteich, Zucht vom 13. Okt. 1958".

LINDEBERG & WIEDERHOLM (1979) pointed out that in describing the chromosomes of *C. acidophilus* Keyl (1960) used the "same material as the adults named as *C. meigeni* Kieffer by THIENEMANN & STRENZKE (1951)". LINDEBERG & WIEDERHOLM suggested that Keyl must have regarded Thienemann & Strenzke's *C. meigeni* as a misidentification for otherwise *C. acidophilus* would be a synonym of *C. meigeni*. In fact, Strenzke (1959, p. 28) himself had doubts about the validity of *C. meigeni* Kieffer, thus in his "Revision der Gattung *Chironomus* Meig. I..." he commented: "Von mehreren Fundplätzen liegen Imagines vor, die sich nicht von dem oben beschriebenen *pseudothummi* unterscheiden lassen. Die zugehörigen Larven weichen jedoch morphologisch und zytologisch z. T. erheblich von einander und von dem *pseudothummi* des typischen Standortes (Knyphauser Wald) ab. Offensichtlich bilden diese Formen, zu denen auch die von THIENEMANN & STRENZKE (1951) als *meigeni* bezeichnete Art aus dem Reinbeker Tonteich bei Hamburg gehört, eine Gruppe von nahe verwandten, ökologisch ähnlich eingestellten Arten oder Unterarten. …" Keyl was clearly aware of this for he wrote in his description of *C. acidophilus* (1960, p. 191): "THIENEMANN UND STRENZKE (1951) glaubten in dieser Form den von Kieffer beschriebenen *Ch. meigeni* erkannt zu haben. Nach STRENZKE (1959) ist die Art *meigeni* wegen Fehlens ausreichender imaginaler Unterscheidungsmerkmale nicht aufrechtzuerhalten".

For light microscope investigation, larval material fixed in 70% alcohol was dehydrated to absolute alcohol and mounted in *Euparal* without hydrolysis. For scanning electron microscopy of larval head structures, whole head capsules or dissected pieces were dehydrated to absolute alcohol, air dried and attached to stubs. Specimens on stubs were coated with a thin layer of gold in a Balzers or SPI sputter coater and viewed with a Philips 500 or Jeol JSM-T 330 SEM.

A cluster analysis incorporated in Version 1.5 of the OZSTAT Data Analysis Package (KENNEDY 1985) with Gower Metric similarity and UPGMA (group average) sorting was carried out on *C. acidophilus* and *C. crassimanus* together with the additional *pseudothummi*-complex species *C. aprilinus* Meigen, *C. dorsalis* sensu Keyl & Keyl, *C. holomelas* Keyl, *C. luridus* Strenzke, *C. melanescens* Keyl, *C. pseudothummi* Strenzke, *C. saxatilis* Wülker *et al.* and *C. uliginosus* Keyl using the eight binary/multistate and eight continuous characters listed in Appendix 1. A data set for the cluster analysis is presented in Appendix 2.

RESULTS

I. TUBULES ON POSTERIOR ABDOMINAL SEGMENTS

Larvae of *Chironomus* are primarily distinguished from those of other genera by the presence of tubular appendages on one or more of the posterior abdominal segments. *C. acidophilus* and *C. crassimanus* both have a pair of rounded ventral tubules on the eighth abdominal segment which are at least equal to segment length and can therefore be classed as long (WEBB & SCHOLL 1985). A pair of lateral tubules on the seventh abdominal segment is present in *C. crassimanus* but as indicated by KEYL (1960), is absent in *C. acidophilus*.

II. HEAD PIGMENTATION

In common with most other members of the *pseudothummi*-complex (WEBB & SCHOLL 1985), the ventral gular and dorsal clypeal regions of head capsules of *C. acidophilus* and *C. crassimanus* are unpigmented.

REVUE SUISSE ZOOL., T. 97, 1990

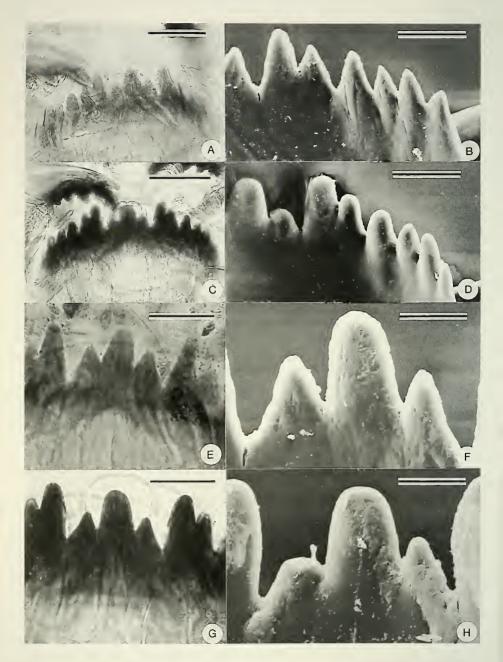


FIGURE 1.

Mental teeth of *C. acidophilus* (A, B, E, F) and *C. crassimanus* (C, D, G, H). (A), (C), (E) and (G) light micrographs; (B), (D), (F) and (H) scanning electron micrographs. Scale lines (A, C) 50 μm; (E, G) 25 μm; (B, D) 20 μm; (F, H) 10 μm.

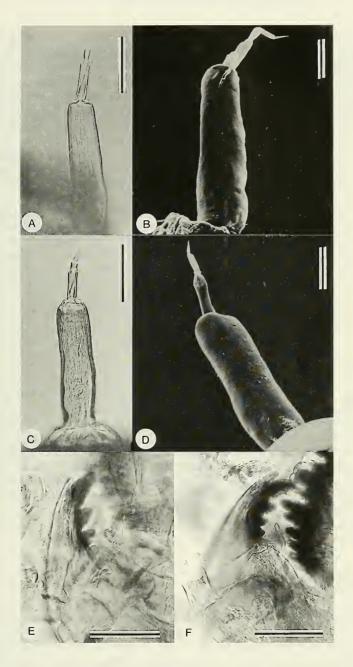


FIGURE 2.

(A-D) Antennae of C. acidophilus (A, B) and C. crassimanus (C, D). (E, F) Mandibular teeth of C. acidophilus (E) and C. crassimanus (F). (A), (C), (E) and (F) light micrographs; (B) and (D) scanning electron micrographs. Scale lines (A, C, E and F) 50 μm; (B, D) 25 μm.

III. MENTAL CHARACTERS

Variation in characters of the mentum (=labial toothplate) observed in C. acidophilus and C. crassimanus is summarized in Table 1. Mental size, assessed by measuring the horizontal distance between verticals through the first lateral teeth, was on average in C. crassimanus the smallest so far recorded in European Chironomus (WEBB & SCHOLL 1985). Mental size is not, however, diagnostic as the range of mental size observed in C. crassimanus overlaps that recorded in other species including C. acidophilus which also has a relatively low mean mental size (WEBB & SCHOLL 1985).

The fourth lateral mental tooth in *C. acidophilus* was either intermediate in size between the third and fifth tooth or approximately the same size as the fifth tooth (Fig. 1), type I and type II respectively in the terminology of WEBB & SCHOLL (1985), while all specimens of *C. crassimanus* examined had type I lateral teeth (Fig. 1).

Type I together with type II, and type I alone, are the commonest conditions of lateral mental teeth observed in European *Chironomus* including all *pseudothummi*-complex species apart from *C. dorsalis* (WEBB & SCHOLL 1985). The commonest type of central mental teeth found in *pseudothummi*-complex species and characteristic of this cytological grouping are, in the terminology of WEBB & SCHOLL (1985), type III and type IV which are characterized by a straight-sided central tooth and flanking teeth which are respectively asymmetrical and symmetrical. In *C. crassimanus* and all but one of the *C. acidophilus* specimens examined, the condition of the central teeth was type III (Fig. 1) while the other specimen had type IV central mental teeth.

IV. MANDIBULAR AND EPIPHARYNGEAL TEETH

WEBB & SCHOLL (1985) recognized three states of coloration of the fourth mandibular tooth: type I, where the tooth is unpigmented; type II, where the tooth is pigmented but less so than the other mandibular teeth; and type III, where the fourth tooth is darkly pigmented and the same color as the other teeth of the mandible. In common with other *pseudothunmi*-complex species, *C. acidophilus* had fourth mandibular teeth with either type I or type II pigmentation (Table 1; Fig. 2) while the fourth mandibular teeth of all *C. crassimanus* examined had type III pigmentation (Table 1; Fig. 2), a state of coloration not previously reported in the *pseudothunmi*-complex (WEBB & SCHOLL 1985).

Variation in number of epipharyngeal teeth in *C. acidophilus* and *C. crassimanus* is summarized in Table 1.

V. ANTENNAE

Antennae of *C. acidophilus* and *C. crassimanus* are illustrated in Fig. 2. The mean length (average length of sclerotized section) of the first and second antennal segments and the mean width of the first segment (measured at the ring organ) were lower in *C. crassimanus* than in *C. acidophilus* (Table 1) and other *pseudothummi*-complex species. However, the range of values of these antennal dimensions observed in *C. crassimanus* (and *C. acidophilus*) overlaps ranges in other species in the *pseudothummi*, *thunmi* and *lacunarius* cytological complexes.

Variation in a number of ratios incorporating antennal dimensions is summarized in Table 1.

TABLE 1.

Variation in head capsule characters * in C. acidophilus and C. crassimanus

mental size (μm) mean±SD (range)	<i>C. acidophilus</i> 54.00 ± 3.59 (47-58)	C. crassimanus 49.78 ± 1.52 (48-52)
condition of		
fourth lateral teeth	5	. 19
I II	5	18
condition of	5	
condition of central teeth		
III	7	18
IV	1	
Pigmentation of		
fourth mandibular tooth		
I	6	_
II	2	_
III	_	18
Number of	-	
epipharyngeal teeth,		
mean \pm SD (range)	13.40 ± 1.52 (11-15)	13.17 ± 1.29 (11-16)
Antennal dimensions		
(μm) mean ± SD (range)		
L1	$121.13 \pm 10.55 (107-144)$	97.83±4.09 (90-105)
L2 W1	30.75 ± 2.55 (27-35)	24.67 ± 1.85 (22-28)
	32.28±1.41 (30-35)	30.39±1.82 (27-33)
Antennal ratios		
mean \pm SD (range) L1/W1	3.57±0.34 (3.50-4.53)	3.22 ± 0.18 (2.90-3.47)
L1/W1 L1/L2	3.96 ± 0.38 (3.56-4.69)	3.98 ± 0.33 (3.60-4.54)
L2/W1	$0.95 \pm 0.10 \ (0.76 - 1.11)$	0.81 ± 0.07 (0.68-0.94)
L1/MS	2.25 ± 0.27 (2.00-2.77)	$1.96 \pm 0.09 (1.83 - 2.10)$
L2/MS	$0.57 \pm 0.08 \ (0.47 - 0.68)$	$0.50 \pm 0.04 \ (0.47 - 0.55)$
W1/MS	0.60 ± 0.04 (0.54-0.68)	0.61 ± 0.04 (0.53-0.67)

* as defined in the text and in WEBB & SCHOLL (1985). L1, length of first antennal segment, L2, length of second antennal segment; W1, width of first antennal segment; MS, mental size

VI. VENTROMENTAL PLATES

As in previously studied species of Chironomus and many other chironomine genera (e.g. PINDER & REISS 1983; WEBB et al. 1985), the ventromental plates of C. acidophilus and C. crassimanus appear as approximately fan-shaped structures lying lateral to the mentum (Figs 3 & 4). Variation in plate size, as indexed by peripheral length (Fig. 3), is summarized in Table 2. The mean size of plates of both C. acidophilus and

C. crassimanus are the smallest so far encountered among European species of *Chironomus* although larger than the average size of plates of some Pacific representatives of the genus (WEBB & SCHOLL 1985, 1987, 1988; WEBB *et al.* 1985, 1987, 1989). Among European *Chironomus*, the range of plate size in *C. acidophilus* overlaps that recorded in *C. crassimanus* and *C. holomelas*, while in addition to *C. acidophilus* the range of plate size in *C. acidophilus* the range of plate size in *C. crassimanus* overlaps that observed in *C. holomelas* and *C. dorsalis* (WEBB & SCHOLL 1985, 1987, 1988; WEBB *et al.* 1985, 1987, 1988).

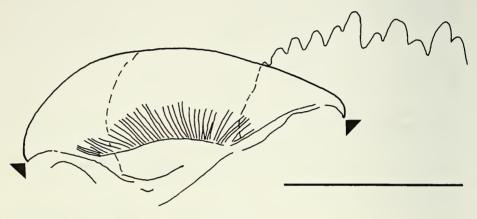


FIGURE 3.

Camera lucida drawing of ventromental plate of *C. crassimanus*. Arrow heads indicate the measured peripheral length. Scale line 100 µm.

In common with most other *Chironomus* species, the outer (ventral) surface of the plates of *C. acidophilus* and *C. crassimanus* is mainly smooth while the inner (dorsal) surface of these plates, as in all previously studied *Chironomus*, is dominated by a series of lamella-like strial ridges arising from an elliptical area of unstriated cuticle occupying the posterior section of the plates (Fig. 4; WEBB *et al.* 1981, 1985, 1987, 1989; WEBB & SCHOLL 1987, 1988). In *C. acidophilus*, this rear section bears some small, irregular folds which are prominent distally (Fig. 4), an arrangement that has been recorded in several *Chironomus* species (WEBB *et al.* 1985, 1987, 1989; WEBB & SCHOLL 1987, 1988), while *C. crassimanus* is unique in having prominent furrows running along the long axis of the unstriated rear section of the inner surface of the plate (Fig. 4).

The range and mean number of striae encountered on plates of *C. acidophilus* and *C. crassimanus* is recorded in Table 2. All specimens of these species had between 40 and 50 striae on their ventromental plates, a range of strial number commonly encountered in European *Chironomus* (WEBB *et al.* 1985). Well developed folding or ridging of extreme distal striae occurred in both *C. acidophilus* and *C. crassimanus* while folding of extreme proximal striae was less prominent in *C. crassimanus* than in *C. acidophilus* (Fig. 5). Ridging of inner- and outermost striae has been observed in a number of other *Chironomus* species (WEBB & SCHOLL 1987, 1988; WEBB *et al.* 1987, 1989). In *C. acidophilus* and *C. crassimanus*, as in previously studied *Chironomus* species (WEBB *et al.* 1985, 1987, 1989; WEBB & SCHOLL 1987), striae become broader and shallower as

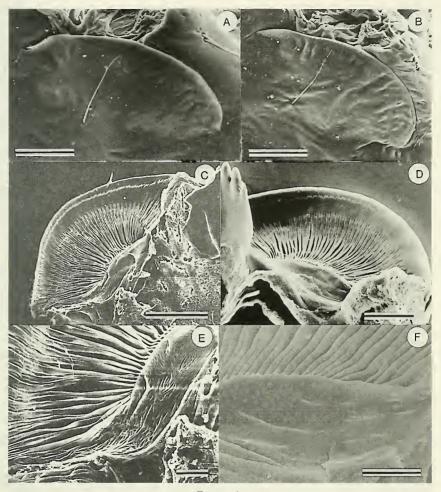


FIGURE 4.

(A, B) Scanning electron micrographs of outer surface of ventromental plates of C. acidophilus (A) and C. crassimanus (B). (D-F) Scanning electron micrographs of ventromental plates of C. acidophilus, inner surface (C), rear section of inner surface (E); C. crassimanus, inner surface (D), rear section of inner surface (F). Scale lines (A-C) 50 μm; (D) 25 μm; (E, F) 10 μm.

they run anteriorly to terminate, without division, well behind the inner of two series of spinous projections that occupy the anterior section of plates (Figs 5 & 6). This type of strial termination, I_A in the terminology of WEBB *et al.* (1985), is the most frequently encountered amongst *Chironomus* species studied to date (WEBB *et al.* 1989).

In common with previously studied *Chironomus* species (WEBB *et al.* 1985, 1987, 1989; WEBB & SCHOLL 1987, 1988), the inner series of spinous projections or hooks comprise a row of mainly small, slender, pyriform spines extending around virtually the complete margin of the plate including the area behind the mentum where inner row spines

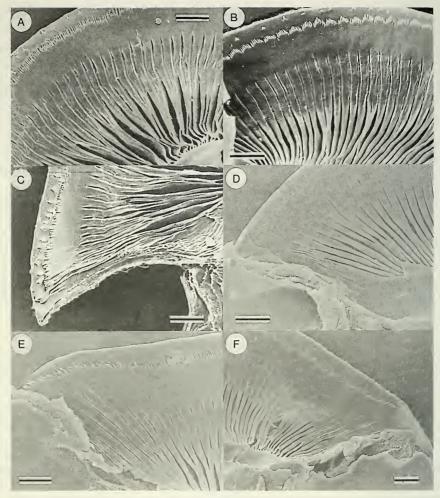


FIGURE 5.

Scanning electron micrographs of inner surface of ventromental plates of *C. acidophilus* mid section (A), distal section (C), proximal section (E); *C. crassinanus* mid section (B), distal section (D), proximal section (F). Scale lines all 10 µm.

progress towards the anterior edge of the plate and become broader or less regular in shape (Figs 6 & 7). Extreme distal members of the inner spine series are also differentiated in morphology being rather larger or broader than the neighbouring spines and in the case of *C. acidophilus*, become confluent with folds on distal striae (Figs 6 & 7). Variation in numbers of inner spines on plates of *C. acidophilus* and *C. crassimanus* is recorded in Table 2. The ranges of inner spine numbers observed in *C. crassimanus* and *C. acidophilus* respectively overlap those recorded in three and four of the six European *Chironomus* species for which information on inner spine numbers is currently available;

LARVAL MORPHOLOGY OF EUROPEAN CHIRONOMUS

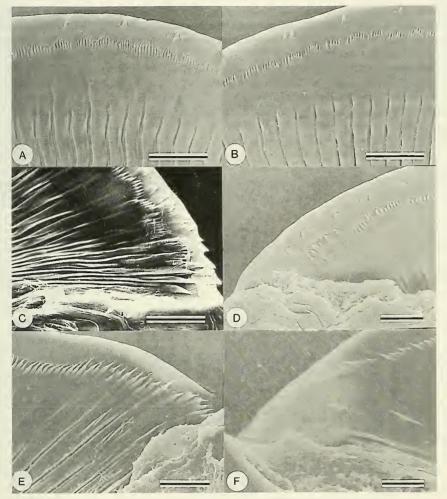


FIGURE 6.

Scanning electron micrographs of ventromental plates of *C. acidophilus* anterio-mid section (A), anterio-distal section (C), anterio-proximal section (E); *C. crassimanus* anterio-mid section (B), anterio-distal section (D), anterio-proximal section (F). Scale lines (A-C, E) 10 μ m; (D, F) 5 μ m.

C. acidophilus and *C. crassimanus* invariably have more inner spines than *C. mendax*. Stora and fewer spines than *C. balatonicus* Devai *et al.* while *C. crassimanus* also consistently has fewer spines in the inner series than *C. pallidivitatus* (Edwards). A small, additional group of pyriform spines situated behind the inner series on the anterior section of proximal striae running under the mentum occurred in both *C. acidophilus* and *C. crassimanus* (Fig. 6). Among European species of *Chironomus*, similar spines have been reported in *C. balatonicus*, *C. montuosus* Ryser *et al.*, *C. pallidivitatus*, *C. storai* Goetghebuer and *C. tentans* (Fabricius) (WEBB & SCHOLL 1987, 1988). In *C. acidophilus* and *C. crassimanus*, as in other *Chironomus* (WEBB *et al.* 1985, 1987, 1989; WEBB & SCHOLL 1987, 1988), spines of the outer series which are situated close to the anterior margin of plates are less numerous than those of the inner row and do not extend as far proximally (Figs 6 & 7). In common with previously studied *Chironomus* species (WEBB *et al.* 1985, 1987, 1989; WEBB & SCHOLL 1987, 1988) outer series spines are broader than inner spines, mainly conical in shape with distal members of the series being broader and more rounded than the rest (Figs 6 & 7). Variation in the number of outer spines in *C. acidophilus* and *C. crassimanus* is recorded in Table 2. The mean number of outer spines in *C. crassimanus* is the third lowest so far recorded among European *Chironomus* although the range of outer spine numbers observed in *C. crassimanus* overlaps those of five other European species including the *pseudothummi*-complex taxa *C. aprilinus, C. dorsalis,* and *C. holomelas* (WEBB *et al.* 1985, 1987; WEBB & SCHOLL 1987, 1988). Among the specimens examined, the number of outer spines in *C. acidophilus* invariably exceeded those in *C. crassimanus* and the

TABLE 2.

Quantitative variation in features of ventromental plates of C. acidophilus and C. crassimanus

	C. acidophilus	C. crassimanus
Size * (µm)	11.(0)	10 (7)
N	11 (6)	10 (7)
range	195.2-243.9	182.0-259.1
mean	220.24	228.16
SD	15.04	18.54
SE	3.14	3.39
Number of striae		
N	12 (7)	12 (7)
range	41-48	40-47
mean	44.83	43.17
SD	2.13	2.17
SE	0.61	0.63
Number of inner spines		
N	9 (6)	5 (4)
range	262-315	238-286
mean	287.11	257.20
SD	207.11	19.72
SE	7.37	8.82
	1.57	0.02
Number of outer spines		
N	8 (5)	5 (5)
range	33-50	21-30
mean	41.13	24.80
SD	5.38	3.70
SE	1.90	1.66
52	1.90	1.00

* peripheral length.

N, number of observations, with number of specimens from which observations were made given in parentheses.

range of outer spine numbers encountered in *C. acidophilus* overlapped those of many other European species including *C. luridus, C. melanescens, C. pseudothummi, C. saxatilis* and *C. uliginosus* in the *pseudothummi*-complex.

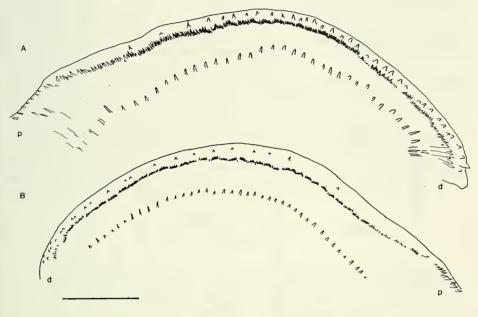


FIGURE 7.

Tracings of scanning electron micrographs of anterior inner surfaces of ventromental plates of *C. acidophilus* (A) and *C. crassimanus* (B). Abbreviations: p, proximal; d, distal. Scale line 25 μ m.

DISCUSSION

In their key to larvae of European *Chironomus* species, WEBB & SCHOLL (1985) made a primary dichotomy on the occurrence of lateral tubules on the seventh abdominal segment. This character also distinguishes *C. acidophilus* and *C. crassimanus*. *C. crassimanus* with lateral tubules, unpigmented clypeus and gula, less than 55 undivided ventromental plate striae, mental size less than 70 µm, and type I fourth lateral mental teeth keys out with *C. luridus, C. pseudothummi* and *C. uliginosus, a group of three morphologically very similar pseudothummi*-complex species. However, *C. crassimanus* is easily distinguished from these species by having a darkly pigmented fourth mandibular tooth (condition III), and a smaller mental size. *C. crassimanus* differs from *C. uliginosus* and most specimens of *C. luridus* and *C. pseudothummi* in having type III rather than type IV central mental teeth while specimens of *C. crassimanus* often have a smaller value of the antennal ratios L2/W1, L1/W1, L1/MS, L2/MS and a greater value of L1/L2 and W1/MS than *C. luridus, C. pseudothummi* and *C. uliginosus*.

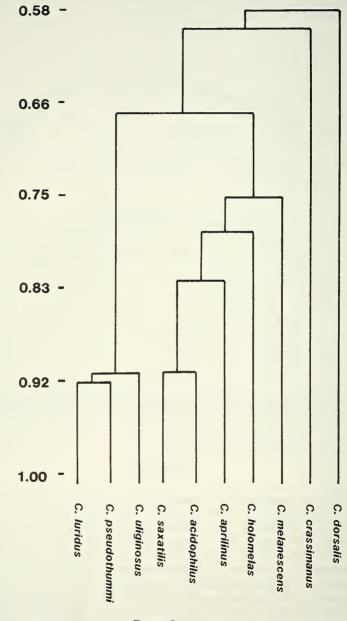


FIGURE 8.

Dendrogram derived from cluster analysis.

similarity

C. acidophilus, in which lateral tubules are absent but with rounded ventral tubules, unpigmented gula and clypeus, type III or IV central mental teeth, pale (type I or type II) fourth mandibular tooth, mental size less than 65 μ m could group with the *pseudothummi*-complex species, *C. saxatilis, C. aprilinus* or *C. holomelas*. However, the minimum size of ventromental plates observed in *C. saxatilis, 256.1* μ m (WEBB, unpublished data) is larger than the maximum size observed in *C. acidophilus*, while L2/W1 is smaller and L1/L2 mostly larger in *C. acidophilus* than in *C. saxatilis. C. aprilinus* is easily distinguished from *C. acidophilus* by larger mental size and the presence of ventral tubules of unequal length, while *C. acidophilus* has substantially more ventromental plate outer spines than *C. holomelas*, undivided ventromental plate striae and higher average values of L1/MS and W1/MS.

In terms of the larval morphology, the phenetic analysis indicates that *C. crassimanus* is relatively distinct from many of the other taxa included in the *pseudothummi*-complex, while *C. acidophilus* groups quite closely with *C. saxatilis*. The relationships of *C. acidophilus*, *C. crassimanus* and the other *pseudothummi*-complex species based on "overall morphological similarity" are not particularly congruent with those derived from karyological and biochemical genetic data (e.g. SCHOLL *et al.* 1980; MARTIN 1979; WÜLKER *et al.* 1981). However this is not an unusual situation among larvae of European species of *Chironomus* (WEBB and SCHOLL, unpublished data) and, as will be argued in more detail elsewhere, probably reflects the occurence of homoplasy.

ACKNOWLEDGMENTS

The authors wish to thank Dr. F. Reiss for the provision of specimens of *C. crassimanus* from the Strenzke collection, the Institute of Anatomy, University of Bern, for the use of SEM facilities and Mr. K. Babl for valuable technical assistance. Dr. H. M. Ryser verified the identification of specimens of *C. acidophilus* by cytotaxonomical criteria.

APPENDIX 1. Characters used in data matrix.

- 1. Lateral tubules on seventh abdominal segment; 1 absent, 2 present.
- 2. Ventral tubules on eighth abdominal segment; 1 equal, 2 unequal.
- 3. Clypeus; 1 pigmented, 2 unpigmented.
- 4. Gula; 1 pigmented, 2 weakly pigmented.
- 5. Mean mental size.
- 6. Most common type of fourth lateral tooth; 1 type I, 2 type II, 3 type III.
- 7. Most common type of central teeth; 1 type III, 2 type IV.
- 8. Pigmentation of fourth mandibular tooth; 1 type I or II, 2 type III.
- 9. Mean number of epipharyngeal teeth.
- 10. Mean length (µm) of first antennal segment.
- 11. Mean length (µm) of second antennal segment.
- 12. Mean width (µm) of first antennal segment.
- 13. Mean size of ventromental plates.
- 14. Mean number of ventromental plate striae.
- 15. Mean number of ventromental plate outer spines.
- 16. Anterior section of striae; 1 divided, 2 undivided.
- 17. Furrows on rear section of ventromental plate; 1 absent, 2 present.

Tava									Chara	Character number	har						Γ
1 0/0	-	~	3	4	5	9	2	ω	9	10	11	12	13	14	15 1	1617	2
C. aprilinus*	-	2	-	-	68.20	-	-	. 	12.93	123.31	28.65	33.38	301.00	46.74	32.26	-	-
C. dorsalis*	2	-	2	2	50.53	e	-	. 	14.62	106.95	27.73	32.86	282.00	39.64	30.22	-	-
C. holomelas*		-	-	-	58.28	2	-	. 	12.46	109.45	32.19	31.40	266.00	44.34	20.93	2	-
C. Iuridus*	2	-	-	-	60.86	-	2		14.83	123.96	35.88	33.08	298.50	50.05	42.00	-	-
C. melanescens*		-	-	-	73.85	-	-	-	13.06	158.06	33.25	41.61	330.00 42.60	42.60	47.75	-	-
C. pseudothummi*	2	-		-	65.33 1		2	-	14.67	14.67 138.68	39.41	35.32	317.50	52.08	36.46	-	-
C. saxatilis*	-	-	-	-	57.27	-	-	-	12.43	12.43 125.20	28.73	35.40	28.73 35.40 271.50 43.07	43.07	39.92	-	-
C. uliginosus*	2	-	-	-	60.77	-	2	-	15.26	139.48	42.71	42.71 33.37	272.50	46.72	38.11	-	-
C. acidophilus	-	-	-	-	54.00 1	-	-	-	13.40	13.40 121.13	30.75	32.28	220.40	44.83	41.13	-	
C. crassimanus	2	-	-	,	49.78	-	-	2	13.17	97.83	24.67	30.39	228.20	43.17	24.80	-	2
																	7

* Data from WEBB & SCHOLL (1985), except characters 13 and 16 for C. saxatilis, (WEBB, unpublished data).

Appendix 2. Data matrix. Numbering and scoring as in Appendix 1

REFERENCES

BRENNAN, A. 1981. Chironomus. Biologist, 28: 133-138.

- FITTKAU, E. J. und F. REISS. 1978. Chironomidae. Pp. 404-440. In: ILLIES, J. (ed.), Limnofauna Europaea (2nd ed). Fischer, Stuttgart.
- KENNEDY, R. B. 1985. OZSTAT A Data Analysis Package for MS-DOS based microcomputers. Unpublished computer software.
- KEYL, H. G. 1960. Die cytologische Diagnostik der Chironomiden. II. Diagnosen der Geschwisterarten Chironomus acidophilus n. sp. und Ch. uliginosus n. sp. Arch. Hydrobiol. 57: 187-195.
 - 1962. Chromosomenevolution bei *Chironomus*. II. Chromosomenumbauten und phylogenetische Beziehungen der Arten. *Chromosoma (Berlin)*, 13: 464-514.
- KEYL, H. G. und I. KEYL. 1959. Die cytologische Diagnostik der Chironomiden. I. Bestimmungstabelle f
 ür die Gattung Chironomus auf Grund der Speicheldr
 üsen-Chromosomen. Arch. Hydrobiol., 56: 43-57.
- LENZ, F. 1954. Tendipedidae (Chironomidae). b) Subfamilie Tendipedinae (Chironominae). B. Die Metamorphose der Tendipedinae. In: LINDER, E. (ed.). Die Fliegen der Palaearktischen Region, 13c, pp. 139-260. E. Schweizerbarth'sche Verlagsbuchhandlung, Stuttgart.
- LINDEBERG, B. and T. WIEDERHOLM. 1979. Notes on the taxonomy of European species of *Chironomus* (Diptera: Chironomidae). *Ent. scand. Suppl.* 10: 99-116.
- MARTIN, J. 1979. Chromosomes as tools in taxonomy and phylogeny of Chironomidae (Diptera). Ent. scand. Suppl. 10: 67-74.
- PINDER, L. C. V. and F. REISS. 1983. 10. The larvae of Chironominae (Diptera: Chironomidae) of the Holarctic region. — Keys and diagnoses. In: WIEDERHOLM, T. (ed). Chironomidae of the Holarctic region. Keys and diagnoses. Part 1. Larvae. — Ent. scand. Suppl. 19: 292-435.
- RYSER, H. M., H. J. GEIGER, A. SCHOLL und W. WÜLKER. 1980. Untersuchungen über die Verbreitung der Zuckmückengattung *Chironomus* in der Schweiz, mit besonderer Berücksichtigung von drei cytologisch nicht beschriebenen Arten. *In:* MURRAY, D. A. (ed.), Chironomidae. Ecology, Systematics, Cytology and Physiology, pp. 17-24. *Pergamon Press, Oxford.*
- RYSER, H. M., A. SCHOLL und W. WÜLKER. 1983. Revision der Gattung Chironomus Meigen (Diptera) VII: C. muratensis n. sp. und C. nudiventris n. sp., Geschwisterarten aus der plumosus-Gruppe. Rev. suisse Zool. 90: 299-316.
- SCHOLL, A., H. J. GEIGER und H. M. RYSER. 1980. Die Evolution der Gattung Chironomus aus biochemisch-genetischer Sicht. In Murray, D. A. (ed.) Chironomidae. Ecology, Systematics, Cytology and Physiology, pp. 25-33. Pergamon Press, Oxford.
- STRENZKE, K. 1959. Revision der Gattung *Chironomus* Meig. I. Die Imagines von 15 norddeutschen Arten und Unterarten. *Arch. Hydrobiol.* 56: 1-42.
- THIENEMANN, A. und K. STRENZKE, 1951. Larventyp und Imaginalart bei Chironomus s. s. Ent. T. 72: 1-21.
- WEBB, C. J. 1980. Modern approaches to the congruence problem in chironomid systematics. In: Murray, D. A. (ed.). Chironomidae. Ecology, Systematics, Cytology and Physiology, pp. 97-104. Pergamon Press, Oxford.
- WEBB, C. J. and J. MARTIN. 1987. The comparative morphology of the larval ventromental plates of Australasien species of *Kiefferulus* (Goetghebuer) and *Nidolorum* Kieffer (Diptera: Chironomidae). Austr. J. Zool. 35: 419-432.

- WEBB, C. J. and A. SCHOLL. 1985. Identification of larvae of European species of Chironomus Meigen (Diptera: Chironomidae) by morphological characters. Systematic Entomology 10: 353-372.
 - 1987. Comparative morphology of the larval ventromental plates of European species of Einfeldia Kieffer and Chironomus Meigen (subgenera Lobochironomus and Camptochironomus) (Diptera: Chironomidae) Ent. scand. Suppl. 29: 75-86.
 - 1988. Ultrastructure of the larval ventromental plates of *Chironomus balatonicus* Devai, Wülker & Scholl (Diptera: Chironomidae). *Mitt. Schweiz. ent. Ges.* 61: 113-121.
- WEBB, C. J., R. S. WILSON and J. D. MCGILL. 1981. Ultrastructure of the striated ventromental plates and associated structures of larval Chironominae (Diptera: Chironomidae) and their role in silk-spinning. J. Zool., London, 194: 67-84.
- WEBB, C. J., A. SCHOLL and H. M. RYSER. 1985. Comparative morphology of the larval ventromental plates of European species of *Chironomus* Meigen (Diptera: Chironomidae). *Systematic Entomology*, 10: 373-385.
- WEBB, C. J., J. MARTIN and W. WÜLKER. 1987. Ultrastructure of larval ventromental plates of European and North American representatives of *Chironomus* Meigen (subgenus *Chaetolabis* Townes) (Diptera: Chironomidae). *Ent. scand.*, 18: 205-211.
- WEBB, C. J., P. S. CRANSTON and J. MARTIN. 1989. Congruence between larval ventromental plate ultrastructure and immature morphology in *Yama* Sublette & Martin and some Oceanin species of *Chironomus* Meigen (Diptera: Chironomidae). *Zool. J. Linn. Soc.* in press.
- WÜLKER, W. 1980. Basic patterns in the chromosome evolution of the genus Chironomus (Diptera). Z. zool. Syst. Evolut.-forsch. 18: 112-123.
- WÜLKER, W., H. M. RYSER und A. SCHOLL. 1981. Revision der Gattung Chironomus Meigen (Dipt.). VI. C. holomelas Keyl, C. saxatilis n. sp., C. melanescens Keyl. Rev. suisse Zool. 88: 903-924.
 - 1983. Revision der Gattung Chironomus Meigen (Dipt.). VIII. Arten mit Larven des fluviatilis-Typs (obtusidens-Gruppe): C. acutiventris n. sp. und C. obtusidens Goetgh. Rev. suisse Zool. 90: 725-745.